

THE DEVELOPMENT OF THE LOOP IN THE JURASSIC BRACHIOPOD *ZEILLERIA LECKENBYI*

by P. G. BAKER

ABSTRACT. An ontogenetic series of *Z. leckenbyi* has been obtained from a locality in the mid-Cotswolds. Serial sectioning has enabled determination of the microstructure and development regime of the loop. The work reveals that a loop of adult character is formed by the time the brachial valve is about 4.0 mm long, confirming Elliott's suspicion that in zeilleriids the early stages of loop development were passed through very quickly. During early development phases the loop is connected to a septal pillar rising from the floor of the brachial valve. The general pattern of loop development appears to combine terebratulid and dallinid characters. It is found that the descending elements play only a subsidiary role during loop development. That they become relatively massive fairly early appears to be due to the fact that they are required to support the ascending complex after resorption of the connection with the median septum has occurred. The growth pattern of the median septum indicates that it may be regarded as a secondary character and therefore makes only a very limited contribution to loop development in the Zeilleriidae. Attention is focused on the gross inadequacy of our knowledge of the actual growth of juvenile loops during the recognized stages passed through during ontogeny. Analysis of the development regime illustrates some of the dangers of recording growth stages which are essentially momentary phenomena in what must necessarily be a cumulative process. The current work indicates that a cryptacanthiini of *Glossothyropsis* type may be ancestral to the Zeilleriidae. It is concluded that the possession of spinose ascending and descending elements is a more important ancestral character than the absence of a median septum and that the microstructure of developing loops will provide the key to the solution of the complex phylogeny of the Terebratulida.

THE loop ontogeny of Terebratulides is not well known and even the more recent interpretations (Dagis 1958, 1959; Babanova 1965) rely heavily on the work of Elliott (1948, 1953). Undoubtedly the main reason for the lack of information is the scarcity of juveniles of representative genera. It is surprising, therefore, that despite our general lack of data, high taxonomic significance is attributed to the loop ontogeny of terebratulides. It appears that microstructural analysis of loop elements will enable some of the gaps in our knowledge to be bridged and that bulk sampling may reveal the presence of very small juveniles previously overlooked.

The material used in these investigations was recovered during the search for micromorphic brachiopod faunas in the Oolite Marl. This deposit is a weakly-coherent interbedded marl and biomicrite of Upper Aalenian (*murchisonae* zone) age occurring in the Inferior Oolite of the mid-Cotswolds around Cheltenham. The two best remaining exposures are at Cleeve Cloud (SO 984261) and Westington Hill Quarry (SP 142368) from which locality the current material was obtained. The stratigraphy of the Oolite Marl and the horizon from which collections have been made are outlined in Baker (1969, p. 388). A third, excellent exposure in the old cutting at Notgrove Railway Station (SP 094213) is now unfortunately no longer available as the area has been taken over for site development.

In addition to a rich organo-detrital residue and micromorphic brachiopods (Baker 1969) the Oolite Marl yields juvenile rhynchonellides and terebratulides and adults assigned to the species *Globirhynchia subobsoleta* (Dav.), *Epithyris submaxillata* (Morris), *Plectothyris fimbria* (Sow.), '*Terebratula*' *whitakeri* Walker MS, and *Zeilleria leckenbyi* (Davidson ex Walker MS).

A collection of 250 juvenile terebratulides, ranging in size from 0.6 to 14.0 mm in length, was analysed on the basis of 27 morphological characteristics. The data obtained from this analysis is too voluminous to be included in the present work and is to be published later. Briefly it may be stated that the larger juveniles may be readily correlated with their adult counterparts and on the basis of character evaluation may also be correlated with progressively smaller juveniles. Fortunately, *Zeilleria leckenbyi* is the only long-looped species present so the possibility of error is greatly reduced.

Thirty specimens ranging from 0.8 to 25.6 mm in length were selected, which, on the basis of the results obtained from morphological analysis, were anticipated to be juveniles and adults of *Z. leckenbyi* (Pl. 82, figs. 1–12). These specimens were serially sectioned and the results obtained are summarized in Table 1. The external morphological characters of all the specimens anticipated to be *Z. leckenbyi* were supported, with only two exceptions, by zeilleriid internal characters. The obvious developmental 'progression' leaves little room for doubt that the remaining 28 shells represent the ontogenetic stages of a single species.

Fundamental to all thinking regarding the interpretation of secondary shell fabric must be the realization that the smaller the unit considered, the closer it must approach Rudwick's (1959) 'momentary' conception of growth and the larger the unit, the closer it approaches his 'cumulative' conception. This means that the various parts of the developing loop are the cumulative product of a series of momentary units. As Westbroek (1967, p. 29) has pointed out, increase in size of internal structures is the result of deposition of shell at their distal ends but thickening is usually the result of shell deposition proximally, i.e. in posterior zones of the shell where structures arise apically. It follows, therefore, that in the apical region of a shell, early growth stages will only be preserved (where no resorption of material has taken place) as cores buried in the shell material of subsequently enlarged structures. Added to this is the problem that growth of the valve must necessarily bring about a change in the orientation of an early structure relative to the commissural plane. As the early growth phases of the pedicle valve are eliminated by resorption in *Z. leckenbyi*, attempts to trace continuity of structures must be based on the study of brachial valves. A consideration of critical importance (Westbroek 1969), apparently largely ignored by many workers, is that owing to the change in orientation of structures during growth, the orientation of the plane of section must be adjusted accordingly if 'buried' structures are to be clearly identifiable in sections of larger shells. For instance, transverse sections through units of the very early cardinalia will be encountered in near horizontal sections through adult shells.

In view of the need for accurate correlation between specimens in different size ranges, trios of specimens were selected which were as near identical as possible, morphologically and in size. Of these, one was retained as a reference, one was sectioned, normal, transverse, and the third specimen was sectioned growth oriented according to the normal transversely sectioned specimen of the preceding size range. In the text, therefore, horizontal sections refer to the orientation of the plane of section relative to the loop rather than to the orientation of the shell, which is usually low oblique. Orientation cannot be exact because the loop is obviously not visible, but critical sections may be correlated to a greater extent using this method. There can be no hard and fast correlation between size of animal and stage of loop development, for at a given size, loop development will

TABLE 1. Tabulation of the structures present in 28 specimens of *Z. leckenbyi* out of a sample of 30 shells anticipated to belong to that species. Of the remaining two shells, one, 1.0 mm long showed no dental plates, the other, 9.0 mm long and having a damaged beak, proved to be a short looped form.

Specimen	Dimensions mm.			Orientation	Internal characters present														Developmnt. phase represented
					Dental plates	Crural plates	Septalium	Median septum	Asc. elements							Desc. elts.		Loop of adult form	
	Septal pillar	Postr. arching spurs	Asc. lamellae						Anterior spurs	Connection with median septum	Lacunae	Asc. branches with spur remnants	Desc. branches	Asc. and desc. elements united	Spinose				
37628/23	0·8	0·7	0·28	H.S.	+														Pre paramagad- iniform
37629/29	0·9	0·8	0·3	H.S.	+														
37630/19	1·2	1·0	0·35	H.S.	+														
37629/9	1·2	1·1	0·4	H.S.	+	+													
37629/4	1·3	1·3	0·4	H.S.	+	+			+										
37629/10	1·3	1·1	0·4	H.S.	+	+													
37629	1·3	1·1	0·4	H.S.	+	+			+										
37589/7	1·5	1·5	0·5	H.S.	+	+			+	+						+			
37630/28	1·7	1·6	0·6	H.S.	+	+		+	+	+	+					+			
37589/3	2·1	2·1	0·7	H.S.	+	+	+	+	+	+	+	+				+			
37556	2·5	2·4	1·1	T.S.	+	+	+	+	+		+	+	+			+			
37570/1	3·0	3·0	1·2	H.S.	+	+	+	+	+		+	+	+				+	+	
37580	3·9	3·4	1·4	T.S.	+	+	+	+	+		+	+	+	+			+	?	
37581	5·0	5·0	1·7	T.S.	+	+	+	+			+	+			+		+	+	
37617	5·4	5·2	1·8	H.S.	+	+	+	+			+				+			?	
37582	5·9	5·4	2·4	H.S.	+	+	+	+			+				+			+	
37583	6·5	6·0	2·5	T.S.	+	+	+	+			+				+			+	
37622	7·2	7·0	3·0	H.S.	+	+	+	+			+				+			+	
37663	10·5	10·4	4·1	H.S.	+	+	+	+										?	
37664	12·2	12·5	5·5	H.S.	+	+	+	+										+	
37665	14·5	14·5	7·3	T.S.	+	+	+	+										+	
37667	17·2	18·5	7·5	T.S.	+	+	+	+										+	
37660	17·5	16·7	8·2	H.S.	+	+	+	+										+	
37657	19·0	18·0	8·0	T.S.	+	+	+	+										+	
37658	19·0	19·0	9·0	H.S.	+	+	+	+										+	
37659	21·0	20·0	9·0	H.S.	+	+	+	+										+	
37661	23·5	20·0	11·0	H.S.	+	+	+	+										+	
37666	25·6	22·0	13·0	T.S.	+	+	+	+										+	

be either precocious or retarded according to the momentary point which has been adopted as the mean. The closest approach to such a correlation must, therefore, lie in the relation of development phases to approximate size categories (Table 1).

Owing to the very small size of the early juveniles and the delicate nature of their loop elements, it was virtually impossible to recognize loop elements in transverse section. This became particularly apparent where the infilling matrix was not of uniform texture. Most of the work was therefore based on horizontal sections. This orientation offered the greatest chance of success as the component fibres of the elements would be more or less length-sectioned and, therefore, more easily visible in the matrix. Traces of transverse sections through specimens are included (text-fig. 1A-C) to conform with the accepted method of illustrating serially sectioned brachiopod loops. However, at this early stage of development the various elements may be only 3-4 fibres thick and do not respond well to photography. For recording loop development photographically, horizontal sections showing length-sectioned fibres yield far better results. Accordingly the evidence provided by horizontal sections has played an important part in the reconstruction of early loops. Those sections which are regarded as critical are also figured (Pl. 84, figs. 1-12).

Acknowledgements. The author is indebted to Dr. J. D. Hudson, Department of Geology, The University of Leicester, for discussion during the preparation of this paper. Thanks are due to Mr. G. McTurk for preparation of the stereoscan negatives and to Professor Sylvester-Bradley for use of the research facilities of the Department of Geology, The University of Leicester.

Registration of Material. The material figured in this paper, together with original and duplicate peels, is to be housed in the Museum collection of the Department of Geology, University of Leicester under the catalogue numbers quoted.

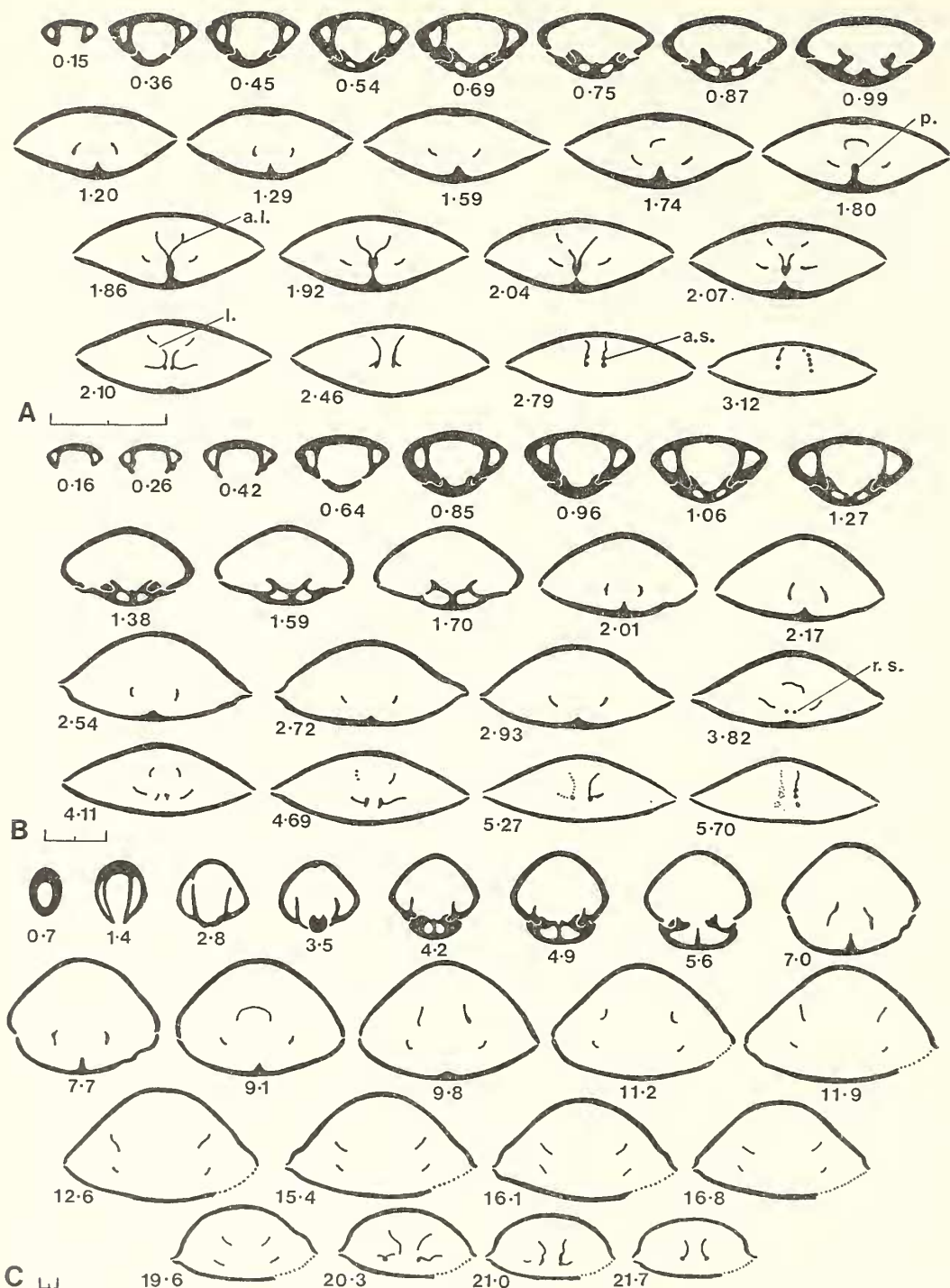
TECHNIQUES AND PREPARATION OF MATERIAL

A comprehensive account of the preparation of Oolite Marl material is given in Baker (1969) and the material studied in the present paper was obtained by the same method. The smaller specimens up to 4.0 mm in length were investigated using the techniques developed for the study of the micromorphic thecidellinid *Moorellina granulosa* (Moore) (Baker 1970). The larger specimens were studied using the techniques developed by Hendry *et al.* (1963).

It has not been possible to locate a separated juvenile brachial valve in which the loop is complete although the bifid appearance of the ascending lamellae is quite common (Pl. 82, figs. 16-18).

NOMENCLATURAL PROBLEMS

This and other studies show that the differences, discussed later, between dallinid and terebratellid loop ontogenies are often very subtle. Although all the changes are variants of two common plans they are complicated by precocious or retarded development and by changes in the relative proportions of the same structures in successive growth stages of a single genus also as a result of changes in the relative proportions of different parts of the loop in different genera. From an evolutionary point of view it is obvious that loop development within the suborder Terebratellidina forms a fairly intimate complex and it would, therefore, be wrong to introduce an entirely new nomenclature for zeillerioid loop



TEXT-FIG. 1A-C. Series of serial transverse sections through specimens of *Z. leckenbyi*, drawn from microprojected cellulose acetate peels, showing features of the species during different phases of development. A. Frenuliform specimen (37580). B. Terebrataliiform specimen (37583). C. Adult specimen (37666). Numbers refer to the distance in mm of the sections from the beak. Lettering as Figs. 3, 4. Scale represents 2 mm.

ontogeny. New terms must be introduced with due regard for their probable affinity with comparable structures in other forms.

Great care has been taken to avoid the use of the term median septum in description of ontogenetic stages as it can be shown that the median septum as observed in the adult *Z. leckenbyi* plays no part in the development of the ascending elements of the loop. Whether the structure plays a valid role in the development of the loops of other terebratulidines is not yet clear.

Muir-Wood (1934) noted that in the Zeilleriidae the septalium is formed by two plates, the septalial plates, which converge and fuse together to form a septum. She states (1934, p. 529) that the septum appears to be distinct from the true median septum in many species. In very young specimens of *Z. leckenbyi* there is no septalium and the plates extending from the crural bases to the floor of the valve (Pl. 82, figs. 14, 15) should, according to the Treatise definition (Williams and Rowell 1965) be regarded as crural plates. Muir-Wood also noted that in *Digonella* the dorsal end of the median septum appears to be inserted in the wall of the brachial valve. Study of oriented valves of *Z. leckenbyi* indicates that both the above structures are represented by the sessile bundle of secondary fibres which gives rise to the septal pillar of this species, in which case the median septum as observed in adult shells is a bi-component subsequent valve element. It post-dates the septal pillar, as the remnant of this structure (Pl. 85, figs. 1, 2) is enveloped as the septum is extended anteriorly. In *Z. leckenbyi*, therefore, the median septum *sensu lato*, makes only a limited, if any, contribution to the development of the ascending elements.

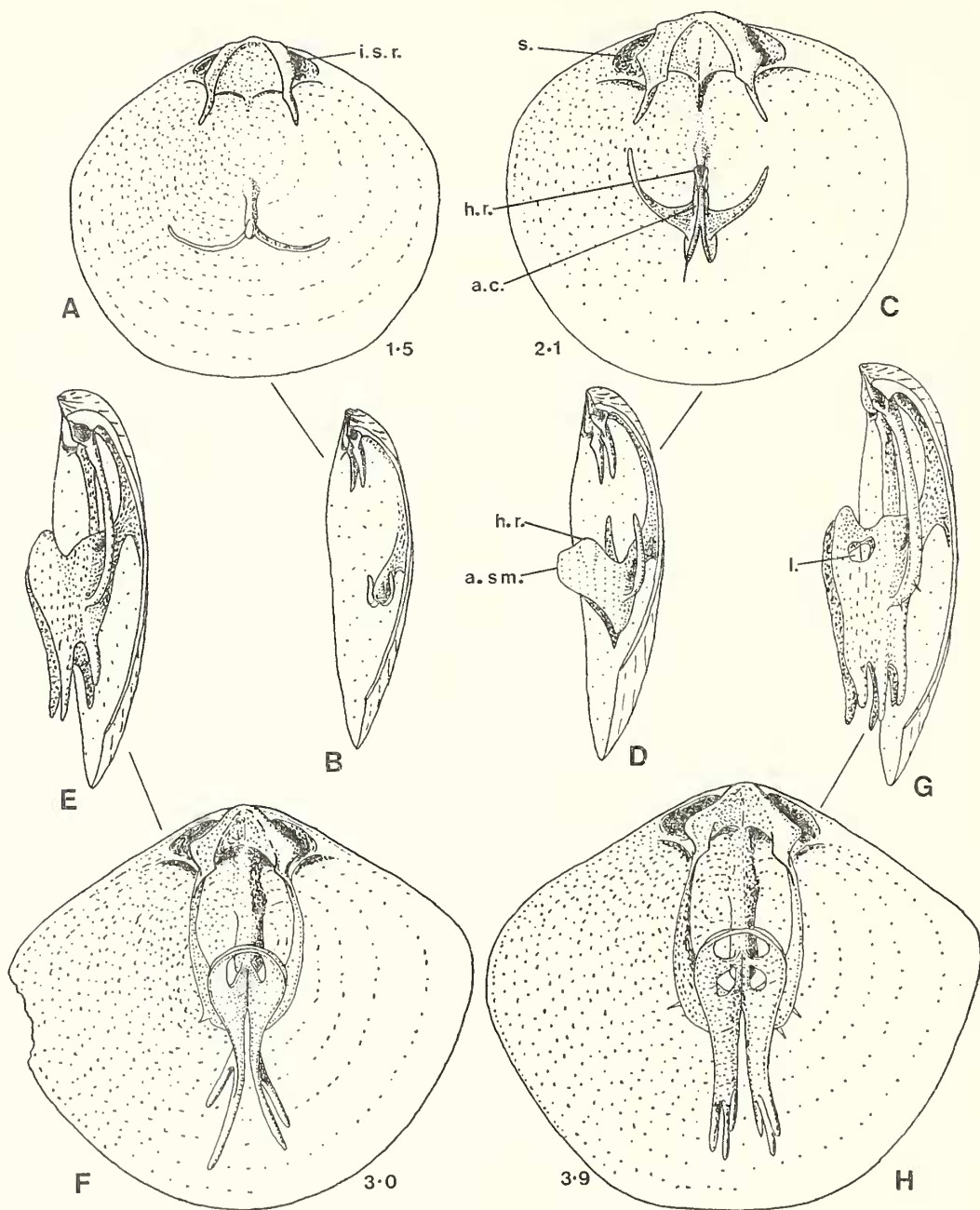
Elliott (1953, p. 263) refers to the often pillar-like upgrowth from the valve floor which constitutes the precursor of the ascending elements in the Terebratulidina. The use of Elliott's term, septal pillar, being most apt, is adopted to describe the almost cylindrical structure arising from the valve floor and leaning anteriorly in a characteristic terebratulid (Elliott 1953, p. 267) manner.

Following the appearance of the pillar the ascending elements develop rapidly and as a number of components appear almost simultaneously the term *ascending complex* is introduced (text-fig. 2C, D). It is felt that this term is required to describe structures which are the precursors of the ascending elements proper (ascending branches and transverse bar) and also those which regulate the early location and anterior extension of the descending branches. The component parts of the axial complex in order of appearance are as follows:

Posteriorly arching spurs. Posteriorly directed outgrowths from the sides of the septal pillar near its distal end. The descending elements unite with them and grow along their ventral edge to fuse with the material of the ascending lamellae which lies between the anterior spurs (text-figs. 2A, B, 3A; Pl. 83, figs. 2, 3).

Ascending septum. Small, vertical, axially aligned plate, developed on top of the septal pillar and replacing the dallinid hood which is sometimes preserved as a rudiment on the posterior edge (text-fig. 2C, D).

Ascending lamellae. A pair of diverging plates which arise from the anterior edge of the ascending septum and are subsequently extended along its ventral edge. These lamellae are the precursors of the ascending branches. As they increase in size they give rise to



horns of material posteriorly, which are deflected towards the mid-line until they unite to form the transverse bar (text-fig. 3B-D; Pl. 83, fig. 6).

Anterior spurs. A pair of prismatic calcite spurs developed from the base of each ascending lamella. They regulate the position of the descending branches relative to the ascending branches and become ensheathed in secondary fibres as the descending branches are extended anteriorly (text-figs. 2E, F, 4, 5; Pl. 83, figs. 1, 8).

From the host of modifications described by Elliott (1953, 1960) and Muir-Wood *et al.* (1965) it becomes clear that terms such as campagiform and frenuliform must not be applied too rigidly. Also the use of the term stage is deplored. It is thought that the term stage is likely to lead to inflexibility as it implies a growth attainment of a momentary nature (Rudwick 1959). Accordingly, the author proposes to use the term *phase* as this suggests the more real, cumulative growth pattern of the loop.

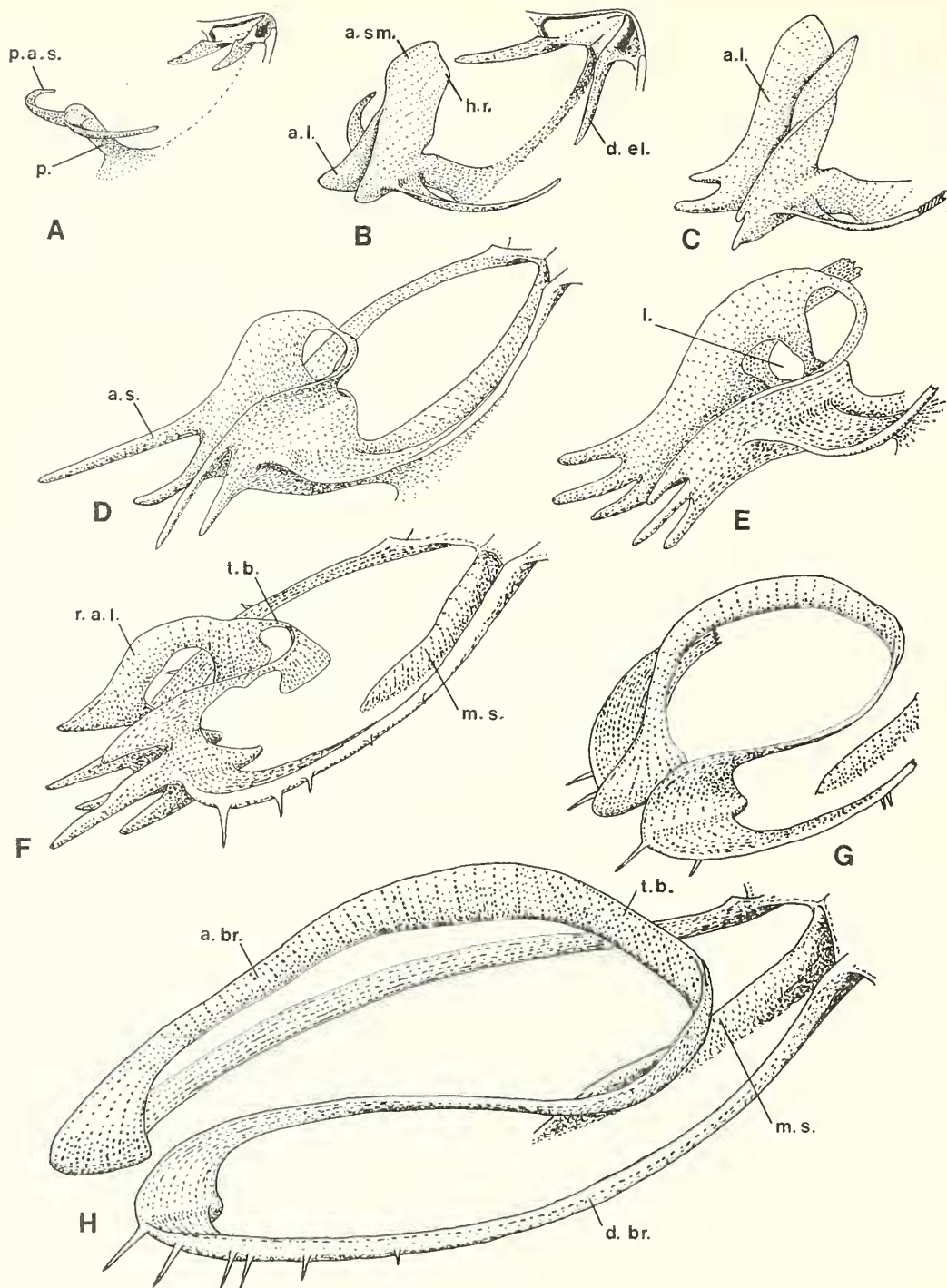
While the ascending complex is developing it shows a close resemblance to the modified magadiniform type seen in *Australiarcula artesiana* Elliott and *Bouchardia rosea* (Mawe) (Elliott 1960). As the microstructure of the magadiniform loop is unknown, the term *paramagadiniform* will be used to describe the loop of *Z. leckenbyi* during this growth phase.

Differences of opinion exist (Thomson 1927; Elliott 1947, 1953) with regard to the correct definition of the campagiform loop, but all specify the presence of a hood. Therefore, by definition *Z. leckenbyi* does not possess a campagiform stage because the hood, even if present, is never more than a rudiment. However, the growth phase succeeding the paramagadiniform culminates in a structure resembling the campagiform loop but arrived at by a different development sequence. Therefore, the phase of development succeeding the paramagadiniform phase will be termed *syncampagiform* to describe the loop of campagiform appearance which arises without the involvement of a hood.

ZEILLERIID DEVELOPMENT PHASES

The developing loop of *Z. leckenbyi* passes through seven recognizable phases of growth, which, on the basis of experience may be anticipated to coincide with certain approximate size ranges.

TEXT-FIG. 2A-H. Reconstructions of early juvenile brachial valves of *Zeilleria leckenbyi* (Davidson). Sequence of interior and lateral views to show the morphology of the developing loop and its prominence relative to the plane of the commissure. The figures are based essentially on data obtained from stereoscanned cellulose acetate peels, but the evidence was reinforced by polished sections and separated valves. A, B. Preparamagadiniform phase (37589/7). A. Brachial view, crural plates sloping down to unite with valve floor. B. Lateral view showing the relatively low pillar with an anterior inclination. C, D. Paramagadiniform phase (37589/3). C. Brachial view showing the form of the ascending complex. Median septum still not properly developed but the anteriors of the crural plates are separating from the valve floor and beginning to form a septalium. D. Lateral view showing the increased development of the descending elements and the ascending complex much higher relative to the commissural plane. E, F. Syncampagiform phase (37570/1). Lateral and brachial views showing the well-developed ascending lamellae, anterior spurs, and transverse bar. Descending branches now united with the sides of the ascending lamellae. Septalium formed and septal pillar enlarged. G, H. Frenuliform phase (37580). Lateral and brachial views showing the location of the lacunae. a.c. ascending complex, a.sm. ascending septum, h.r. hood rudiment, i.s.r. inner socket ridge, l. lacuna, s. dental socket. Numbers refer to the length of the shell in mm from which the peels were obtained.



TEXT-FIG. 3. Series of three-quarters profile reconstructions (not to scale) of the loop of *Z. leckenbyi* showing the various elements in the complete development sequence. A. Preparamagadiniiform. B, C. Early and late magadiniiform. D. syneampagiiform. E. Frenuliform. F. Terebrataliiform. G. Dalaliniform. H. Zeilleriiform. Figs. C, E, G show only the distal portions of the descending branches. a.br. ascending branch, a.l. ascending lamella, a.s. anterior spur, a.sm. ascending septum, d.br. descending branch, d.el. descending element, h.r. hood rudiment, l. laeuna, m.s. median septum, p. septal pillar, p.a.s. posteriorly arching spur, r.a.l. resorbed ascending lamella, t.b. transverse bar.

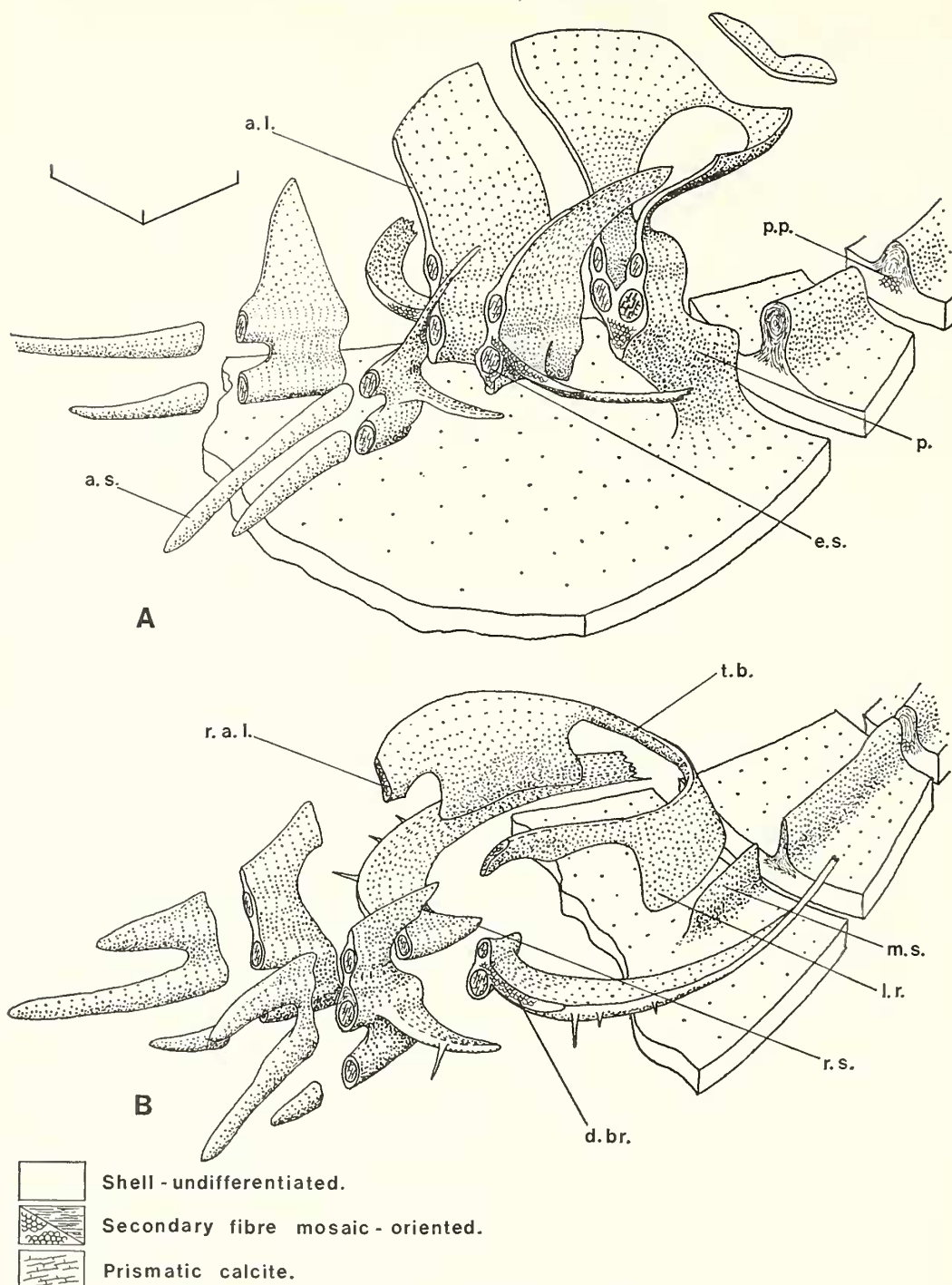
Phase 1. Pre-paramagadiniform. It seems probable that the floor of the brachial valve is at first featureless. The precursor of the ascending elements of the loop appears very early as a bundle of fibres, longitudinally arranged, lying almost parallel with the floor of the valve (Pl. 83, fig. 11). Growth increments are added to the ventral surface of this bundle, as might logically be expected from the position it occupies on the valve floor. An abrupt change in this growth pattern occurs when the animal is about 1.3 mm long. The bundle of fibres becomes re-oriented to rise as a septal pillar projecting from the valve floor (text-fig. 2A, B; Pl. 82, figs. 13–15). This change in fibre orientation is accompanied by a change in growth pattern as the new growth increments are now added anteriorly, i.e. on the originally dorsal surface of the fibre bundle (Pl. 83, figs. 9, 10). The explanation for this change is obvious, for the new development regime will carry the developing loop anteriorly.

Soon after the formation of the septal pillar, two ribbons of calcite, arched posteriorly, arise laterally at a point close to its distal end (Pl. 83, figs. 2, 3, 5; text-fig. 2A, B, 3A). The descending elements at this time are very short. Before the shell reaches a length of 1.8 mm a further development phase begins.

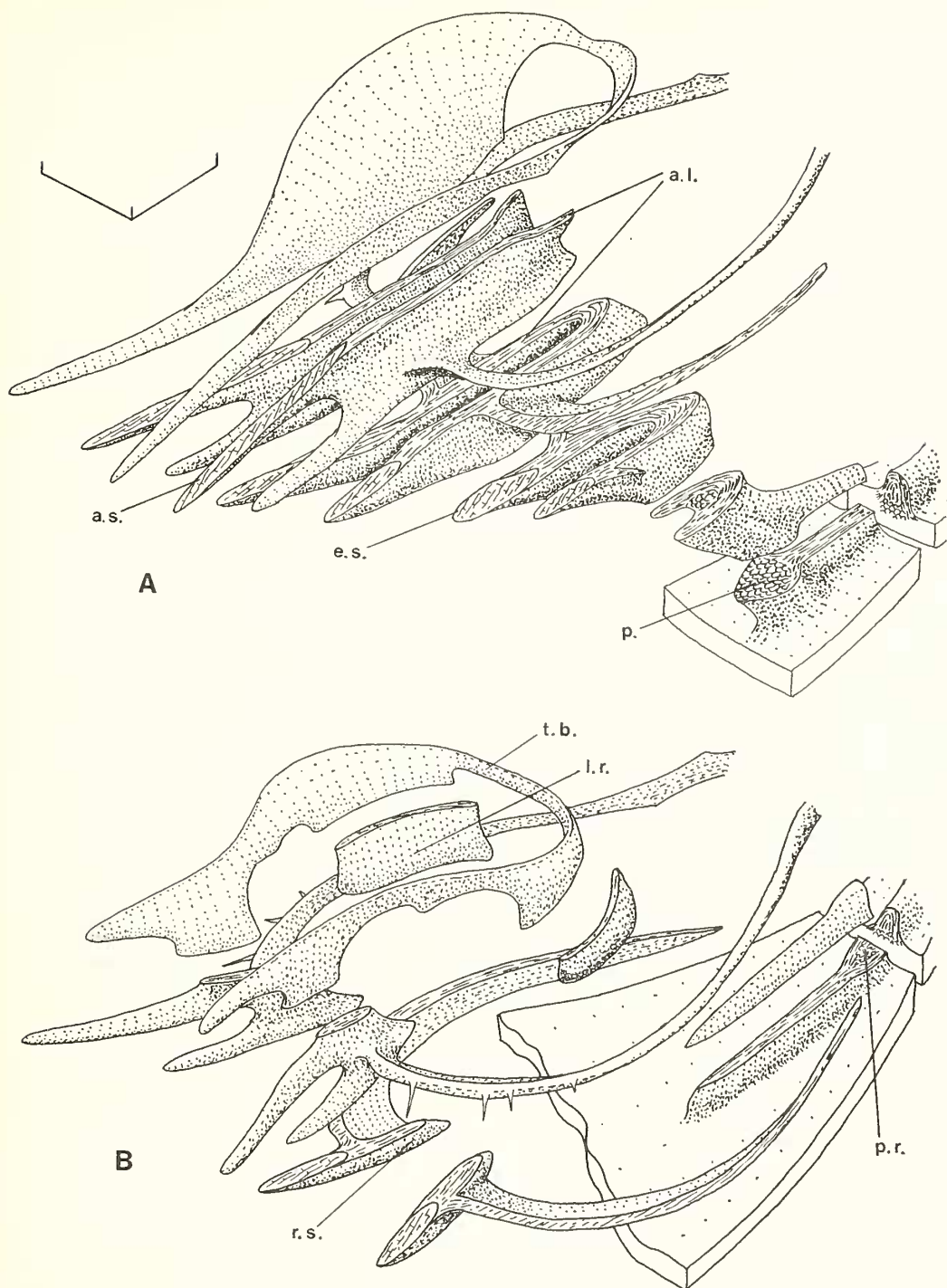
Phase 2. Paramagadiniform. Shell length 1.8–2.5 mm. The distal end of the septal pillar becomes laterally flattened and rises vertically as an ascending septum (text-figs. 2C, D, 3B). The descending elements become more strongly developed and there is a proportionate increase in the size of the posteriorly arching spurs, so that the two soon unite. A swelling appears about half way up the posterior edge of the septum. On occasional specimens this may be seen to develop into a low ring-like collar at its distal end. The structure actually plays no part in the formation of the loop but may be interpreted as a rudimentary hood of the type found in *Austriarcula artesiana* Elliott. At the same time two divergent lamellae, the ascending lamellae, develop at the anterior edge of the ascending septum (Pl. 82, fig. 18, Pl. 83, fig. 6; text-fig. 3B, C). During this phase of development the crural plates become raised above the floor of the valve. In the mid-line they become turned down to form a shallow septalium (Pl. 82, fig. 17) and extend as an overlay of secondary fibres above and on either side of the earlier deposited fibre bundle which represents the sessile portion of the septal pillar (Pl. 83, fig. 11). The divergent lamellae are of the utmost importance for they represent the precursors of the whole of the subsequently developed loop. Within each lamella arise the proximal ends of a pair of spurs which herald what is fundamentally the most important phase of development of the entire loop.

Phase 3. Syncampagiform. Shell length 2.5–3.5 mm. No direct evidence is available but it is believed that the ascending lamellae extend up the anterior edge of the ascending septum and along its ventral edge, at first diverging and subsequently converging posteriorly to form the rudiment of the transverse bar of the adult loop (text-fig. 3B–D). This mode of origin is favoured because the campagiform hood is never more than a rudiment and the transverse connection when first formed is always thread-like.

Following the initiation of the spurs (occasionally three on each lamella) their development proceeds rapidly and is accompanied by thickening of the distal ends of the descending branches and broadening of the ascending lamellae so that the loop becomes relatively massive (text-figs. 2E, F, 3D). Investigation shows that the anterior spurs are composed of prismatic calcite (Pl. 83, fig. 4; text-figs. 4, 5). As they are extended



TEXT-FIG 4. Serial block reconstructions to show the microstructure of the loop of *Z. leckenbyi* as it appears in transverse section during the syncampagiiform, A, and terebrataliiform, B, phases of development. For the purposes of clarity only the distal portions of the descending branches are included. a.l. ascending lamella, a.s. anterior spur, d.br. descending branch, e.s. enveloped spur, l.r. lamella remnant, m.s. median septum, p. septal pillar, p.p. pillar precursor, r.a.l. resorbed ascending lamella, r.s. resorbed spur, t.b. transverse bar. Scale represents 0.2 mm.



TEXT-FIG. 5. Serial block reconstructions to show the microstructure of the loop of *Z. leckenbyi* as it appears in horizontal section during the syncampagiiform, A, and terebrataliiform, B, phases of development. Lettering as in Fig. 4, except p.r. pillar remnant. Scale represents 0.2 mm.

anteriorly, they are responsible for controlling and facilitating the location of the descending branches (Pl. 83, figs. 1, 8). The spurs act as girders for the anterior extension of the descending branches, becoming at first partially, then completely enveloped by secondary fibres as the descending elements are extended (text-figs. 4, 5). The culmination of this development phase is the development of a structure which morphologically bears a close resemblance to the dallinid campagiform stage. At the moment, however, there is no data on the dallinid type to show whether the two forms are microstructural equivalents.

EXPLANATION OF PLATE 82

Figs. 1–18. Stereoscan photomicrographs, except 10–12, of various specimens of *Z. leckenbyi* (Davidson) from the Oolite Marl, Westington Hill Quarry near Chipping Campden, showing the general morphology during ontogeny. Specimens coated with evaporated aluminium before photography. 1–3. Brachial, anterior, and lateral views of a preparamagadiniform juvenile (37629). Note the rounded appearance of the brachial valve and the beginning of apical resorption of the delthyrium during this phase of development. $\times 35$. 4–6. Lateral, brachial, and anterior views of a syncampagiform juvenile (37530). Apical resorption is now advanced and a low anterior sulcus is present. $\times 15$. 7–9. Anterior, brachial, and lateral views of a terebrataliiform juvenile (37581). Brachial valve now becoming more elliptical. $\times 8$. 10–12. Brachial, lateral, and anterior views of an adult (37668) for comparison purposes. $\times 1$. 13. Interior of a brachial valve (37671) during the preparamagadiniform phase of development, showing the septal pillar rudiment in the floor of the valve prior to the formation of the median septum. $\times 18$. 14. Three-quarters profile view of specimen (37671) showing the septal pillar rudiment and crural plate (arrowed) descending to the valve floor. $\times 50$. 15. Interior of a brachial valve (37672) showing the septal pillar rising from the valve floor. The crural plates are more well developed but still united with the valve floor. $\times 20$. 16. Interior of a brachial valve (37669) showing the median septum and septal pillar with divergent ascending lamellae. $\times 18$. 17. Three-quarters profile view of specimen (37669) showing the crural plates now raised above the floor of the valve and forming a shallow septalium. $\times 45$. 18. High incidence profile view of specimen (37584) showing the ascending lamellae. The loop of this specimen is clearly damaged and was probably syncampagiform or frenuliform. $\times 12$.

EXPLANATION OF PLATE 83

Figs. 1–11. Stereoscan photomicrographs of specimens of *Z. leckenbyi*. Material for all figures, except figs. 2, 3, obtained from cellulose acetate peels coated with evaporated aluminium before photography. 1. Montage of a horizontal section through a syncampagiform ascending lamella (37570/1, 12) showing the anterior spur, a.s., ensheathed in secondary fibres posteriorly and 'locating' the fibres of the descending element (arrowed). $\times 500$. 2. Photomicrograph, reflected light, of a horizontal section through a polished specimen (37589/3) showing the posteriorly arching spurs arising from the septal pillar. $\times 40$. 3. Retouched copy of fig. 2. 4. Transverse section through an anterior spur of a frenuliform specimen (37580/102) showing the prismatic calcitic core. $\times 525$. 5. Micrograph of a peel obtained from the etched surface of specimen (37589/3), fig. 2 above, enlarged to show detail of the junction of the posteriorly arching spurs with the septal pillar. $\times 180$. 6. Horizontal section through a paramagadiniform specimen (37589/11) showing the ascending septum and divergent ascending lamellae arising from its anterior edge. $\times 70$. 7, 8. Transverse sections through the anterior spurs of the left, fig. 7, and right, fig. 8, ascending lamellae of specimen (37580) showing the enveloped prismatic cores and their controlling influence on the location of the descending branches, fig. 8, centre. $\times 200$. The actual separation between the left and right lamellae at this magnification would be approximately 65 μm . 9. Horizontal section through a syncampagiform specimen (37570/1, 7) showing the septal pillar in near transverse section with the change in the orientation of the secondary fibres anteriorly. $\times 100$. 10. Enlarged view of the anterior portion of the septal pillar shown in fig. 9, to show detail of the fibre mosaic. $\times 275$. 11. Montage of a transverse section through a frenuliform specimen (37580/48) showing the septal pillar precursor fibre bundle (arrowed) overlain by secondary fibres as a result of the anterior extension of the median septum. $\times 300$.



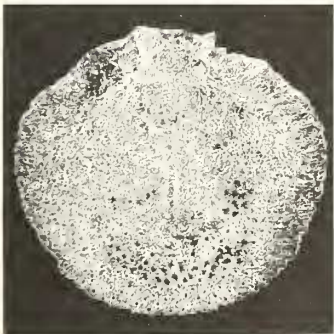
1



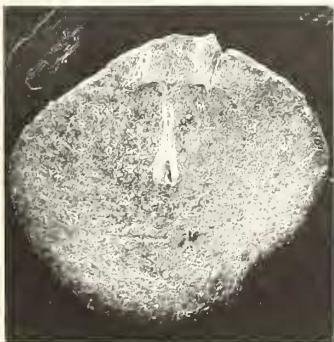
2



7



13



16



3



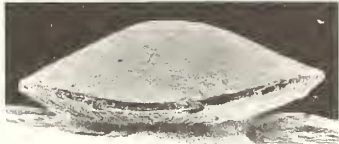
4



5



8



6



9



10

11

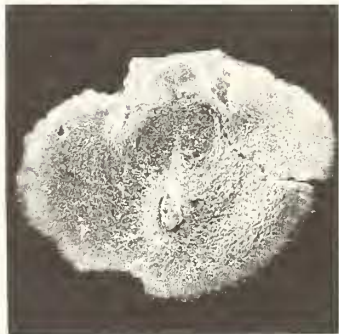
12



14



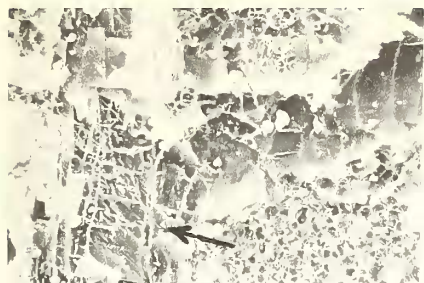
17



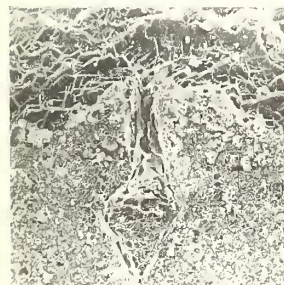
15



18



1

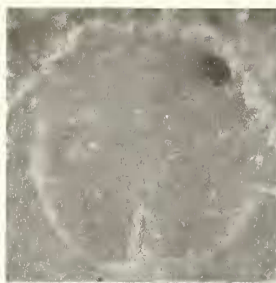


9



10

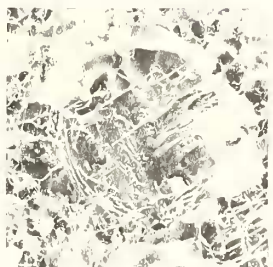
11



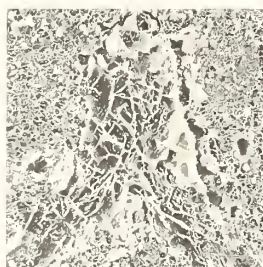
2



3



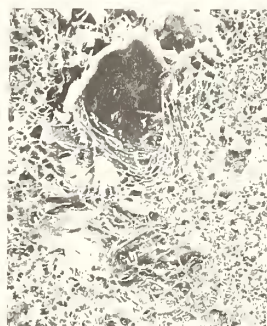
4



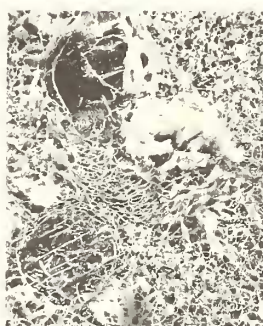
5



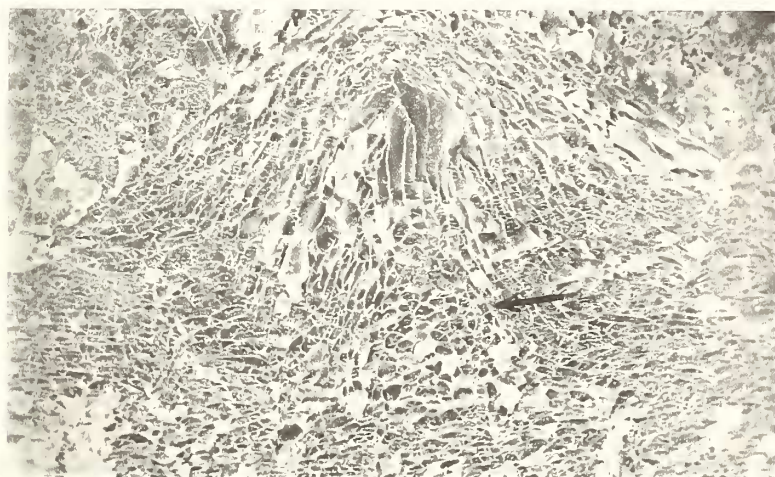
6



7



8



11

Subsequently deposited material continues to accumulate posteriorly in the mid-line of the valve to form a recognizable median septum which is extended anteriorly so that the septal pillar itself becomes partially enveloped (Pl. 83, fig. 11; text-figs. 4, 5). Although this has a strengthening effect on the pillar the primary objective appears to be the provision of a base for the attachment of adductor muscles.

Development through the three phases described may be regarded as being aimed at the attainment of a basic skeletal structure which is capable of being translated into a loop able to support a plectolophe. Metamorphosis of this existing framework is necessary to elaborate and alter the relative proportions of the various loop elements produced by the initial development regime. Shell resorption, until now not a prerequisite of loop development, quite suddenly assumes a critical role in current and all subsequent development.

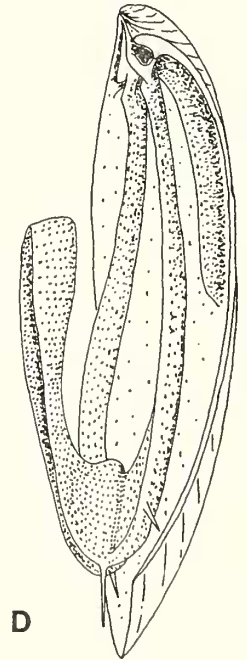
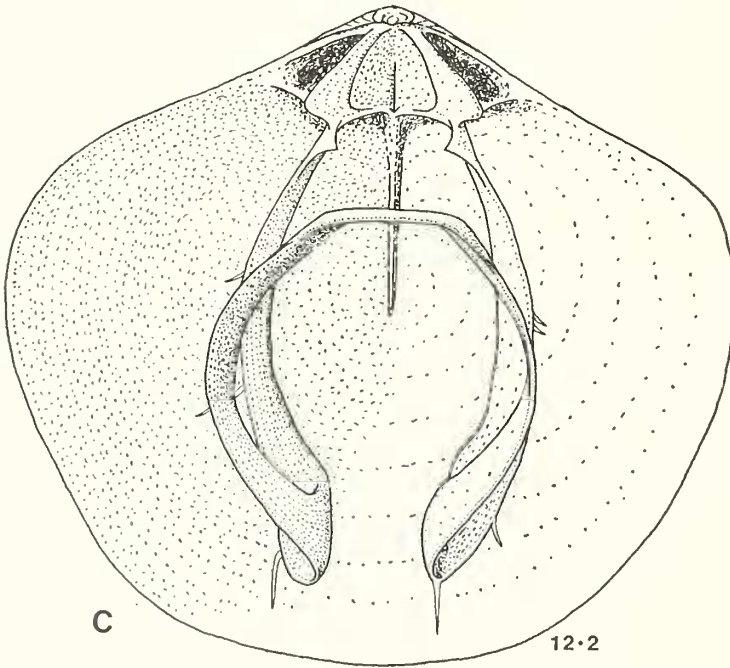
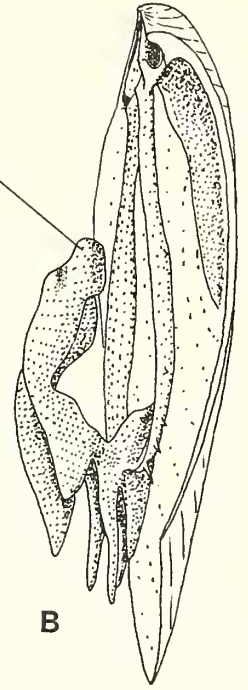
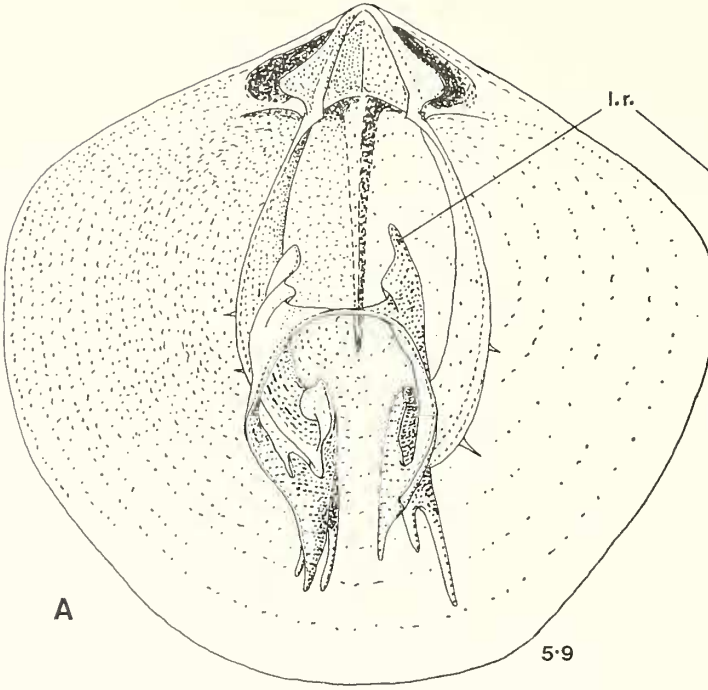
Phase 4. Frenuliform. Shell length 3.5–4.0 mm. Although this phase of development probably does not reflect any change in the form of the lophophore it does illustrate that important physiological changes are taking place. Whilst the anterior of the loop is developing in the manner described above, resorptive activity begins at the posterior of the ascending complex. Two lacunae appear close to the point of divergence of the ascending lamellae (text-figs. 2G, H, 3E).

Phase 5. Terebrataliiform. Shell length 4.0–7.2 mm. As the lacunae increase in size the distal portion of the pillar is also resorbed so that the loop becomes freed from its connection with the septal pillar (text-figs. 3F, 6A, B). None of the material sectioned showed the retention of a connection between the descending branches and the septal pillar so that a form corresponding to the true terebrataliiform stage of the dallinids has not been seen in *Z. leckenbyi*. However, if the mechanics of resorption are considered it seems probable that the delicate strips of material posterior to the lacunae would be lost before the descending branch connections and it is therefore logical to assume a short terebrataliiform phase. It is the intimate relationship between the processes of accretion and resorption which during this phase sculpture the approximate configuration of the adult loop.

The anterior spurs have by now apparently fulfilled their purpose as they cease to develop although their remnants are still visible (Pl. 85, fig. 3; text-fig. 3F) and these continue to regulate the development of the descending branches. Apparently, the posterior end of the lower spur of each lamella is resorbed more slowly as forms passing through this phase of development normally show a small, posteriorly pointing projection, posterior to the point of union of the lamella with the descending elements.

Resorption, after it has begun, apparently proceeds rapidly as the transition from syncampagiform to late terebrataliiform is accomplished quickly and as far as can be ascertained, during the time that the shell is between 3.5 and 7.2 mm in length.

The median septum continues to extend anteriorly after resorption of the connection of the septal pillar with the ascending elements has occurred. The pillar remnant, enveloped by subsequently deposited fibres, can be clearly seen in horizontal sections through young shells, some distance from the anterior termination of the median septum (Pl. 85, figs. 1, 2). The median septum, therefore, as seen in zeilleriids must be regarded as a median septum *sensu lato*.



Phase 6. Dalliniiform. Shell length 7.2–19.0 mm. The dalliniiform phase of development is essentially concerned with smoothing out the irregularities of the crudely adult loop developed during the preceding development phase. The loop thus formed (text-figs. 6C, D, 3G), although quite symmetrical is still relatively heavy and the anterior of the ascending branches still has a plate-like aspect.

Phase 7. Zeilleriiform. Shell length > 19.0 mm. The culmination of the accretion–resorption regime produces an adult loop in which all the elements are comparatively slender and ribbon-like (Ager 1956) with the descending branches often densely spinose (text-fig. 7A, B). The growth and resorption zones of the adult loop show the same basic pattern as that illustrated by Williams (1968, p. 25) in *Magellania flavescens* (Lamarck). The main difference lies in the fact that the spinose zones of the descending branches of the adult loop of *Z. leckenbyi* consist of a double ribbon of shell material (Pl. 85, figs. 4, 6). The spines develop in the same manner as the anterior spurs and show a similar fibre enveloped prismatic core (Pl. 85, fig. 5).

DEVELOPMENT OF SPINES

Occasional spines appear on the descending elements even during the syncampagiiform phase but they only become numerous during the late dalliniiform phase. The development of spines is considered by Elliott to be indicative of some power of secretion of calcite by cirri. In *Z. leckenbyi* the spines can be shown to be a fundamental part of the loop. At first it was thought that the spines might be ‘unused’ anteriors of spurs which had become isolated by resorption and owed their orientation to rotation of the loop axis during growth. Later it was realized that the spurs always lie relatively close to the mid-line of the valve and could in no way migrate to the observed position of the spines on the descending elements. It appears, therefore, that the spines and spurs follow the same pattern of development. The implication of this will be discussed later.

FUNCTION OF THE LOOP

From a consideration of Rudwick’s work (1962) on filter-feeding mechanisms in brachiopods. It seems certain that during the pre-paramagadiniiform growth phase the brachial apparatus supported a schizolophe and that during the paramagadiniiform phase

TEXT-FIG. 6A–D. Reconstructions of juvenile brachial valves of *Z. leckenbyi*. The figures are based essentially on data obtained from stereoscanned cellulose acetate peels but the evidence was reinforced by polished sections and separated valves. A, B. Brachial and lateral views of a late terebrataliiform shell (37582). All connections with the septal pillar have been resorbed. The descending branches are relatively massive and the ascending branches and transverse bar are differentiated. The ascending lamellae are now only represented by unresorbed lamella remnants, i.e. The loop rises very high above the commissural plane, almost touching the floor of the pedicle valve. The septalium is fully developed and the median septum is formed by the rapid extension of the septalial plates to envelop and extend beyond the remains of the septal pillar. C, D. Brachial and lateral views of a typically dalliniiform early adult loop (37664). The descending branches, ascending branches, and transverse bar are of relatively massive proportion. The anterior spurs have by now been eliminated by resorption. The anterior extension of the median septum is relatively slower and the lateral profile of the loop is becoming flatter. Numbers indicate the length in mm of the shell from which the peels were obtained.

it supported a zygolophe. As the ascending lamellae diverged and the transverse bar appeared, the zygolophe would develop into a plectolophe.

At the beginning of the syncampagiform phase material is added rapidly to the descending elements so that the descending branches become relatively massive. It seems that the posterior projections from the ascending complex provide an initial framework for the accelerated development of the descending elements, i.e. they act as 'formers' to enable the descending elements to progress rapidly but the directive control over the morphology of the anterior of the loop is exercised by the ascending elements.

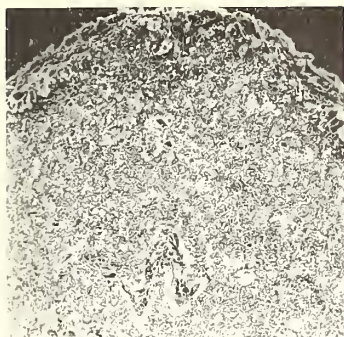
Elliott (1953) suggests that selection pressure is directed towards the development of a more efficient lophophore and the fact that most terebratulide loops are believed to have supported a plectolophe indicates that this form of organization was in some way advantageous to the animal. Elliott further maintains that any mutation favouring the earlier attainment of an adult pattern of lophophore would be selected and correlates this with the advantages conferred by earlier attainment of an adult loop. As in *Z. leckenbyi* the anterior spurs and spines follow the same development pattern it seems probable that they appeared as undifferentiated structures on the descending and ascending elements of ancestral forms. At some point in time, possibly under the influence of strong selection pressure certain spines on the ascending elements could be 'fortuitously' utilized for the extension of the descending branches and, therefore, for the increase in size of the loop. The importance of a mutation which enabled the animal to utilize the anterior spines in a locating role, as a means for rapidly extending the anterior portion of the loop, will be readily appreciated.

EXPLANATION OF PLATE 84

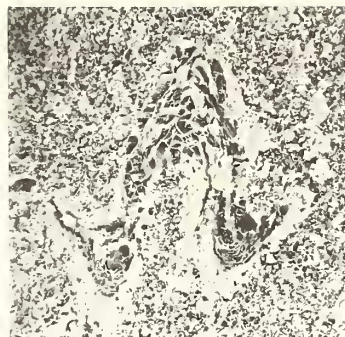
Figs. 1-12. Stereoscan photomicrographs of cellulose acetate peels of selected horizontal serial sections through a juvenile *Z. leckenbyi* (37570/1) showing the various elements of the syncampagiform loop. Peel interval 20 μ m. Material of all figures coated with evaporated aluminium before photography. 1. Ascending lamellae and connection with the dorsal edge of the descending branches. Peel 10, $\times 40$. 2. Enlarged view of the ascending complex shown in fig. 1. $\times 120$. 3, 4. Ascending lamellae with the anterior spurs beginning to develop. Peel 11, original and retouched copy, $\times 110$. 5, 6. Ascending lamellae with the lower anterior spurs and descending branches. Peel 12, original and retouched copy, $\times 70$. 7, 8. Descending branches (left one with spine) beginning to extend along the spurs. Peel 14, original and retouched copy, $\times 50$. 9, 10. Ascending lamellae separated, with the upper anterior spurs almost reaching the anterior margin of the shell. Peel 25, original and retouched copy, $\times 36$. 11, 12. Ascending lamellae united posteriorly to form the transverse bar. Peel 32, original and retouched copy, $\times 20$.

EXPLANATION OF PLATE 85

Figs. 1-6. Stereoscan photomicrographs of *Z. leckenbyi*. Material for all figures obtained from cellulose acetate peels coated with evaporated aluminium before photography. 1. Horizontal section through the median septum of an early terebrataliiform specimen (37617/7). $\times 45$. 2. Montage of an enlarged portion of the proximal end of the septum shown in fig. 1, to show the pillar remnant enveloped by the development of the septum. $\times 260$. 3. Montage of the point of union between the ascending and descending elements, upper right, of a late terebrataliiform specimen (37582/25) showing the remnant of the anterior spur, lower centre. Horizontal section. $\times 275$. 4. Enlarged portion of fig. 6 showing the detail of the prismatic inner, left, and fibrous outer, right, double ribbon of the descending branches of the loop. $\times 265$. 5. Montage of a horizontal section through a portion of a descending branch of an adult loop (37661/13) showing the prismatic core of a spine sectioned obliquely. $\times 260$. 6. Montage of a horizontal section through a portion of the distal end of a descending branch of an adult loop (37661/11) showing the prismatic inner ribbon repeatedly deflecting the outer fibrous ribbon to form cored spines. Arrow indicates anterior of loop. $\times 105$.



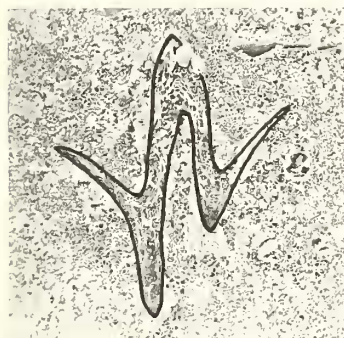
1



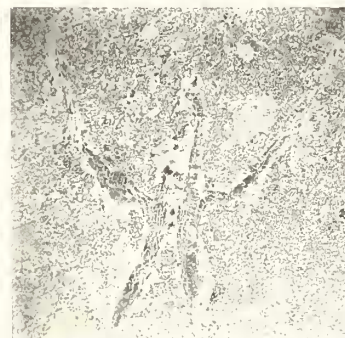
2



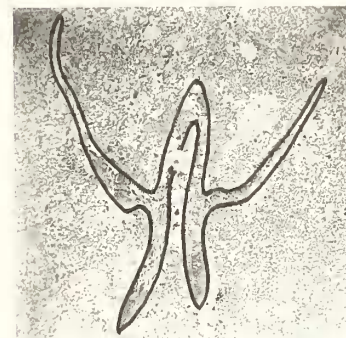
3



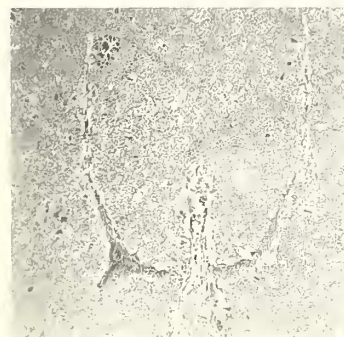
4



5



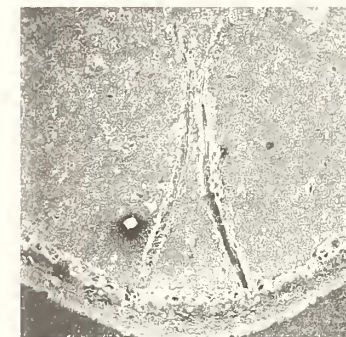
6



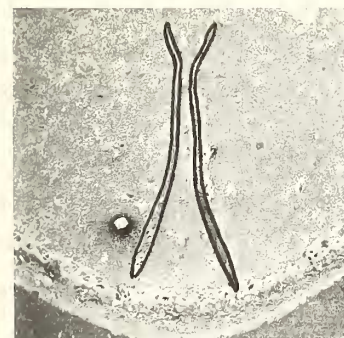
7



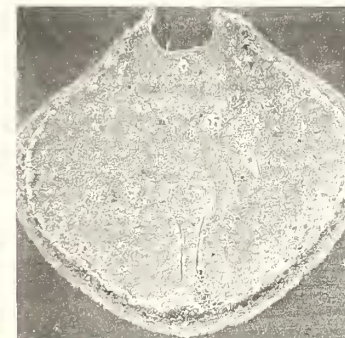
8



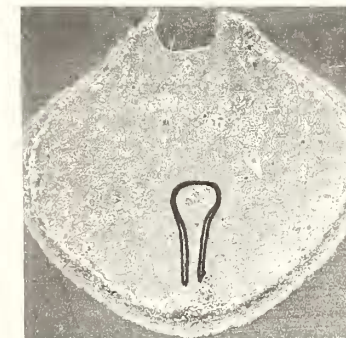
9



10



11



12

BAKER, Zeilleriid loop

